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GEOGRAPHIC VARIATION IN MORPHOLOGY OF ALASKA-BREEDING BAR-TAILED GODWITS (*LIMOSA LAPPONICA*) IS NOT MAINTAINED ON THEIR NONBREEDING GROUNDS IN NEW ZEALAND

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Abstract.—Among scolopacid shorebirds, Bar-tailed Godwits (*Limosa lapponica*) have unusually high intra- and intersexual differences in size and breeding plumage. Despite historical evidence for population structure among Alaska-breeding Bar-tailed Godwits (*L. l. baueri*), no thorough analysis, or comparison with the population's nonbreeding distribution, has been undertaken. We used live captures, field photography, museum specimens, and individuals tracked from New Zealand to describe geographic variation in size and plumage within the Alaska breeding range. We found a north–south cline in body size in Alaska, in which the smallest individuals of each sex occurred at the highest latitudes. Extent of male breeding plumage (proportion of nonbreeding contour feathers replaced) also increased with latitude, but female breeding plumage was most extensive at mid-latitudes. This population structure was not maintained in the nonbreeding season: morphometrics of captured birds and timing of migratory departures indicated that individuals from a wide range of breeding latitudes occur in each region and site in New Zealand. Links among morphology, phenology, and breeding location suggest the possibility of distinct Alaska breeding populations that mix freely in the nonbreeding season, and also imply that the strongest selection for size occurs in the breeding season. *Received 7 October 2010, accepted 7 February 2011.*

Key words: Alaska, Bar-tailed Godwit, geographic variation, *Limosa lapponica baueri*, morphometrics, New Zealand, plumage.

La Variación Geográfica en la Morfología de los Individuos de *Limosa lapponica* que se Reproducen en Alaska no se Mantiene en los Sitios No Reproductivos en Nueva Zelandia

Resumen.—Entre las aves playeras escolopácidas, *Limosa lapponica* presenta diferencias intra e intersexuales inusualmente altas en tamaño y plumaje nupcial. A pesar de la evidencia histórica de la estructura poblacional entre los individuos de *L. l. baueri* que se reproducen en Alaska, no se ha realizado ningún análisis profundo ni comparación con la distribución de la población no reproductiva. Empleamos capturas de aves vivas, fotografías de campo, especímenes de museo e individuos seguidos desde Nueva Zelandia para describir la variación geográfica en tamaño y plumaje dentro del rango reproductivo de Alaska. Encontramos un gradiente norte-sur en tamaño corporal en Alaska, en el cual los individuos más pequeños de cada sexo se encontraron a las mayores latitudes. La extensión del plumaje reproductivo de los machos (proporción de las plumas de contorno no reproductivas reemplazadas) también aumentó con la latitud, pero el plumaje reproductivo de las hembras fue más extensivo a latitudes intermedias. Esta estructura poblacional no se mantuvo en la estación no reproductiva: la morfometría de las aves capturadas y la fecha de las partidas migratorias indicaron que individuos de un amplio rango de latitudes reproductivas se presentaron en cada región y sitio de Nueva Zelandia. Los vínculos entre la morfología, fenología y localización reproductiva sugieren la posibilidad de poblaciones reproductivas distintivas en Alaska que se mezclan libremente en la estación no reproductiva y también implican que la fuerte selección por tamaño se da en la estación reproductiva.

Within the breeding range of many species, individuals exhibit geographic variation in morphology, appearance, or behavior, reflecting either inherited or environmental differences (Zink and Remsen 1986). In migratory species, differential migration patterns within an apparently continuous geographic range (e.g., "leapfrog" or "chain" migration systems) may create stable population segregation (Lundberg and Alerstam 1986) and, potentially, breeding isolation, promoting population structure and phenotypic diversification (Mayr 1963). Therefore, spatial distribution of individuals throughout the entire annual cycle may indicate the strength of population structure, and may also reveal where differential selection for phenotypic traits occurs.

The Bar-tailed Godwit (*Limosa lapponica*; hereafter "godwit"), a long-distance migratory shorebird, breeds in a discontinuous

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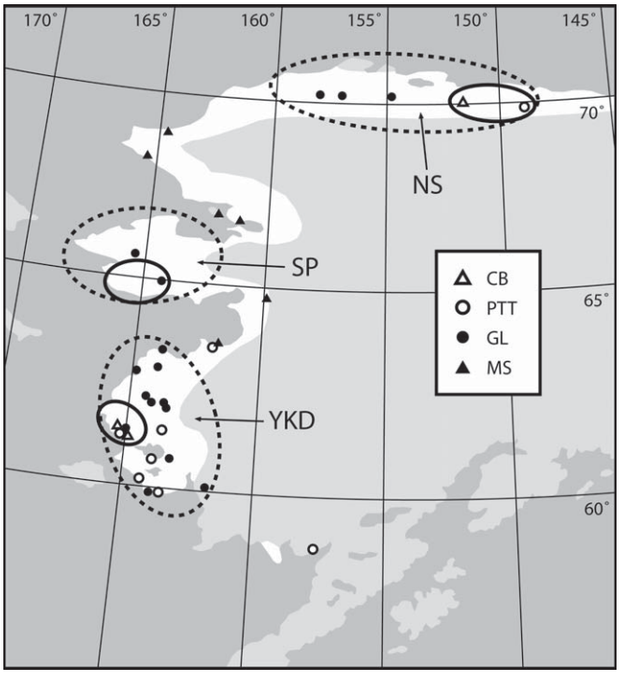

Fig. 1. Alaska breeding locations of Bar-tailed Godwits in this study. Dashed ellipses indicate three main regions used for geographic comparisons (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope). Solid ellipses indicate sites of godwit captures and field photography. CB = resights of godwits color-banded in New Zealand (n = 3). PTT = godwits tracked from New Zealand using satellite telemetry (n = 8). GL = godwits tracked from New Zealand using geolocators (n = 16). MS = sites of museum specimens collected outside the three main regions. Unshaded area indicates known breeding range (McCaffery and Gill 2001).

band of Arctic and sub-Arctic tundra from Scandinavia east to Alaska. There are four recognized subspecies (from west to east: *L. l. lapponica*, *taymyrensis*, *menzbieri*, and *baueri*; Engelmoer and Roselaar 1998) and a small, isolated population in far-eastern Russia of uncertain taxonomic status (purported *L. l. anadyrensis*; Engelmoer and Roselaar 1998, Tomkovich 2010). These populations have distinctive migratory routes, timing of migration, and morphology (Rynn 1982, Engelmoer and Roselaar 1998).

Although the sexes are similar in nonbreeding plumage, male godwits grow much more striking breeding plumage than females, resulting in unusually dramatic sexual plumage dimorphism among scolopacid shorebirds (Jukema and Piersma 2000: their figure 1). Size dimorphism in godwits (larger females) is also remarkably high among monogamous shorebirds that share incubation and parental care (McCaffery and Gill 2001). In addition, significant individual variation in both plumage and size occurs within each sex. In particular, individuals undergo substantially different degrees of presupplemental contour-feather molt (from very little to >90%), which results in conspicuous variation in breeding plumage (Piersma and Jukema 1993).

The subspecies *L. l. baueri* breeds in western and northern Alaska (Fig. 1) and migrates >10,000 km to nonbreeding grounds in New Zealand and eastern Australia (McCaffery and Gill 2001). Field observations suggest geographic variation within Alaska: males with the greatest extent of breeding plumage were absent from southern breeding sites, but arrived later than local breeders and passed through these areas en route to northerly breeding areas (McCaffery et al. 2011). This agrees with data from Alaska museum specimens, in which males collected north of 64°N latitude had a greater extent of breeding plumage and were smaller than southern males (Rynn 1982). Distinct strategies in timing of molt and fueling among premigratory godwits in New Zealand also support the possibility of multiple breeding populations within *L. l. baueri* (Battley and Piersma 2005).

Recently, godwits tracked on migration with light-sensitive geolocators shed further light on population structure: males departing New Zealand with a greater extent of breeding plumage arrived later in Alaska, and later-arriving birds of both sexes bred farther north (Conklin et al. 2010). In fact, breeding latitude was linked with timing of every stage of northbound migration, as well as with postbreeding departure from Alaska. It is thus plausible that breeding latitude may influence the distribution of individuals in the nonbreeding season, but this hypothesis has yet to be tested.

Here, we describe population structure within the breeding range of *L. l. baueri* and ask whether this structure persists in the nonbreeding season. We examined geographic variation in size and plumage of both sexes within Alaska, using museum specimens in conjunction with capture, photography, and tracking of live birds. For comparison, we examined historical capture data within New Zealand to describe the population structure by morphology across a similar range of latitude in the nonbreeding season.

Methods

Morphometric and Plumage Data

Morphometrics.—For live captures, we report culmen (mm; exposed length), wing chord (mm; maximum flattened), and mass (g); not all measurements were available for all captures. Despite numerous observers, we assume insignificant systematic observer bias. Godwit mass undergoes drastic seasonal changes; for New Zealand captures, we report mass only for captures during October to mid-December, when nonbreeding mass is relatively stable (Wilson et al. 2007, P. F. Battley and J. R. Conklin unpubl. data). For Alaska captures, we pooled masses taken during incubation and brood rearing, although data are lacking on breeding-season mass changes.

For museum specimens, we measured length of exposed culmen (mm); all measurements were taken by J.R.C. On the basis of expected post mortem shrinkage of 1.69% (Engelmoer and Roselaar 1998: table 6), we corrected culmen lengths of museum specimens for direct comparison with live culmen measurements.

Plumage.—Beginning in January, godwits molt from nonbreeding ("basic") to breeding plumage, in partially overlapping "prealternate" and "presupplemental" contour-feather molts (Jukema and Piersma 2000), the latter of which appears to affect only ventral regions. In general, males undergo much more extensive presupplemental molt than females, but there is substantial individual variation in both sexes. Ventral alternate plumage typically features lateral barring on a pale background, whereas supplemental

feathers are reddish and lack barring (Jukema and Piersma 2000). Therefore, we characterized ventral breeding plumage as the extent of red supplemental feathers visible against a pale background of basic and/or alternate feathers. We visually estimated proportion (in 5% increments) of red feathers in three ventral regions: "vent" (posterior ventral plumage from leg to vent); "breast" (anterior ventral plumage from leg to upper breast); and "throat" (ventral plumage above breast to chin).

Dorsal plumage appears to undergo only one prebreeding molt: basic feathers are plain gray with a dark central stripe, whereas alternate feathers are blackish brown with pale or reddish spotting on the edges (McCaffery and Gill 2001). We estimated "dorsal" (mantle and scapulars, not including wing coverts) breeding plumage as the proportion (in 5% increments) represented by dark, spotted feathers.

The extent of ventral alternate barring varies among individuals, and the amount of barring still evident during the breeding season depends on the extent of presupplemental molt that is subsequently completed. We scored barring in the anterior ventral region as follows: 0 = no barring; 1 = barring on flanks only; 2 = barring on flanks and upper breast; and 3 = barring on flanks, breast, and belly.

To remove potential observer differences, all plumage was scored from photographs by J.R.C. Depending on available photographs, not all plumage regions were scored for every individual. To gauge the comparability of different photographic sources (see below), we conducted a blind scoring trial using individuals photographed both free-living and in-hand during the same week (n = 13); 92% of scores differed by ≤10%, and there was no consistent directional bias in plumage scores. Therefore, we combined plumage scores from all data sources for analysis.

Bill color.—Bill color of godwits varies seasonally: nonbreeding birds have predominantly pinkish bills that darken to black at the distal end, whereas bills of breeding birds are mostly black. From photographs of live godwits in Alaska, we scored bill color as the proportion (in 5% increments) of both mandibles that looked black. We excluded museum specimens because of potential post mortem changes in bill color.

Sources of Data

Museum specimens.—From three collections of godwit specimens, we examined breeding individuals (n = 70; 40 male, 30 female) collected from 1891 to 2001 in Alaska (60.4–71.3°N). To exclude passage birds, we included only birds collected at known breeding areas from late May to late July or recorded as exhibiting breeding behavior. We photographed specimens using standardized lighting and multiple angles, to enable scoring of plumage at a later date.

Live captures.—We compiled morphometric data from adult godwits captured during incubation or brood rearing at breeding sites in Alaska (61.8–70.0°N; Fig. 1) during May–July of 2005–2010 (n = 57; 30 male and 27 female). We compiled morphometric data from adult godwits captured at nonbreeding sites in New Zealand (34.5–46.6°S; Fig. 2) during late September to early April of 1987–2010 (n = 1,807; 932 male and 875 female). Godwits were aged on the basis of plumage (McCaffery and Gill 2001); we excluded birds of unknown age and those aged <3 years. Godwits were sexed by culmen length, plumage, or both. Females are generally larger than males (culmen > 99 mm = female; < 90 mm = male), but intermediate birds (culmen = 90–99 mm) cannot be sexed by size alone.

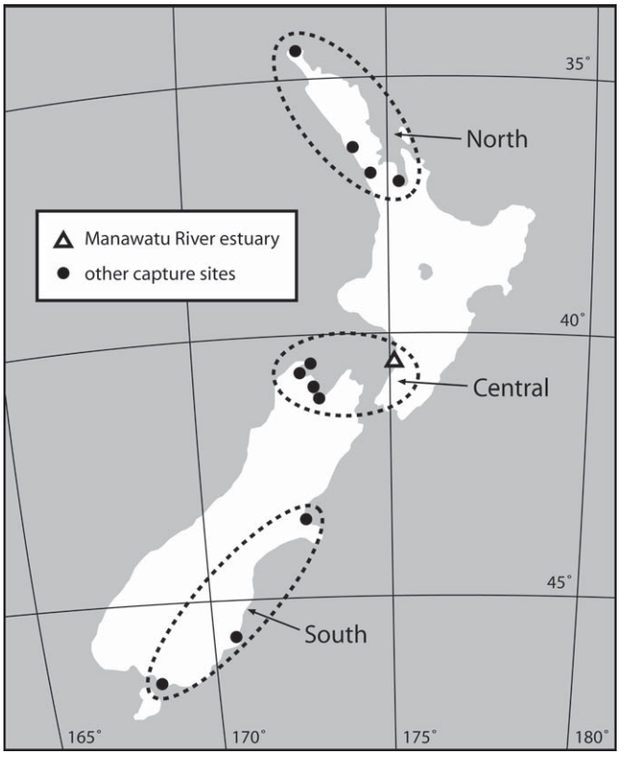

Fig. 2. New Zealand capture sites of nonbreeding Bar-tailed Godwits. Dashed ellipses indicate three main regions used for geographic comparisons.

Plumage enables subjective sexing when supplemental plumage is present (January–October): greater extent and richer red color indicate male. However, we estimate that 1–2% of godwits in the New Zealand sample may be incorrectly sexed (P. F. Battley and J. R. Conklin unpubl. data).

Some godwits captured in New Zealand were tracked to Alaska breeding sites using satellite telemetry (n = 8; P. F. Battley et al. in prep.), geolocators (n = 16; Conklin et al. 2010), or color-band resightings (n = 3). Consequently, morphometric data from these individuals occur in both Alaska and New Zealand data sets.

Field photography.—To collect plumage data from free-living godwits in Alaska, we visited known breeding areas near Nome, on the Seward Peninsula (64.5–65.2°N, 164.8–166.7°W), and south of Deadhorse, on the north slope of the Brooks Range (69.7–70.1°N, 148.7–151.5°W; Fig. 1) during June to early July 2009. We conducted walking surveys, digitally photographing all breeding individuals encountered. We used geographic positioning system (GPS) locations, times, and individual characteristics (e.g., bill length and unique plumage traits) to avoid pseudoreplication of individuals.

Biologists involved in prior field work (2003–2009) provided photographs of free-living godwits from numerous Alaska breeding sites (58.8–70.5°N), plus in-hand photos of 8 godwits captured at three sites on the Yukon-Kuskokwim Delta National Wildlife Refuge (61.1–61.4°N, 165.4–165.6°W; Fig. 1). The final data set of live photographs included 123 Alaska godwits (72 male and 51 female; median = 11 photos bird^{-1}, range: 1–135).

Migratory departures from New Zealand.—At the Manawatu River estuary, New Zealand (40.47°S, 175.22°E; Fig. 2), we monitored departures in a small population of godwits (200–280 individuals; ~25% were individually color-banded). Using direct observation and digital photography, we recorded exact time and individual membership of departing flocks during three migration periods (4 March–5 April, 2008–2010). We conducted daily high-tide surveys to confirm remaining flock size and presence of marked godwits; daily resighting probability of marked birds was >95%. As a result, departures of marked birds were known to the day in 84% of cases, and for the remaining 16% we are confident of accuracy within ±1 day. Geolocator data (Conklin et al. 2010) confirmed that observed departures from the estuary matched departure from New Zealand. We determined departure dates for 76 marked godwits (36 male and 40 female); for individuals monitored in multiple years, we averaged departure dates across available years.

Analysis.—Although godwits breed in a nearly continuous band of coastal tundra in Alaska from near the Canadian border in the northeast to Bristol Bay in the southwest (McCaffery and Gill 2001; Fig. 1), for logistical reasons most field work (including all live captures and photographs in this study and most historical collection) has been conducted in three discrete regions (Fig. 1): Yukon-Kuskokwim Delta (YKD; 59.7–63.3°N, 161.8–166.2°W), Seward Peninsula (SP; 64.4–65.8°N, 162.3–166.7°W), and North Slope (NS; 69.6–71.3°N, 148.4–160.1°W). For comparison, we divided godwit captures in New Zealand into three regions separated by >200 km (Fig. 2): "North" (34.5–37.2°S), "Central" (40.4–41.3°S), and "South" (43.5–46.6°S).

Because of differences in size and plumage, we considered the sexes separately in our analyses. For each morphometric variable, we examined geographic variation using single-factor analysis of variance (ANOVA), and Tukey's post hoc test for between-region differences. For plumage variables and bill color, we used Kruskal-Wallis nonparametric ANOVA, and Tamhane's post hoc test.

Museum specimens offered a more continuous representation of the breeding range than capture and field photography (Fig. 1). In addition, two New Zealand-captured females were tracked to breeding areas outside the three Alaska regions. For these reasons, Alaska totals and sample sizes for some tests exceed the sums for the three regions. We examined the association between breeding latitude and culmen length (pooled live and corrected museum culmen lengths) using linear regression, and compared male and female regression coefficients using Student's t (Zar 1999). For male plumage variables, we pooled the three regions with specimens collected elsewhere in Alaska ($n = 13$), and examined associations with breeding latitude using linear regression.

Results

Morphometrics

Female godwits are much larger than males, on average (Tables 1 and 2), despite overlap in bill length, wing chord, and body mass (t-tests; all measures for both Alaska [AK] and New Zealand [NZ]: $P < 0.0001$). Body proportions also differed by sex: females had

Table 1. Geographic variation in morphometrics of breeding adult Bar-tailed Godwits in Alaska. Data from live captures only, including New Zealand godwits tracked to Alaska breeding sites. Significant results in among-region ANOVA are indicated in bold. Asterisk indicates significant result in between-region post hoc test ($P < 0.05$). Abbreviations: YK = Yukon-Kuskokwim, SP = Seward Peninsula, and NS = North Slope.

		All Alaska			YK Delta			Seward Peninsula		
		n	Mean	Range	*n*	Mean	SE	*n*	Mean	SE
Male	Culmen (mm)	38	84.6	71.3–94.0	21	88.0	0.94	7	83.6	0.96
	Wing (mm)	37	232.3	218–243	20	235.2	1.30	7	231.7	1.21
	Wing/culmen	37	2.76	2.45–3.20	20	2.68	0.03	7	2.77	0.03
	Mass (g)	29	255.7	205–326	16	269.9	5.07	5	238.8	9.90
Female	Culmen (mm)	46	108.0	88.5–125.5	25	114.2	1.10	4	106.8	1.25
	Wing (mm)	44	244.7	228–261	25	249.0	1.14	4	241.5	1.89
	Wing/culmen	44	2.28	2.02–2.73	25	2.18	0.02	4	2.26	0.03
	Mass (g)	28	319.4	265–384	12	339.7	6.63	4	294.5	9.98

		North Slope			ANOVA			Tukey post hoc		
		n	mean	SE	*F*	df	*P*	YK–SP	YK–NS	SP–NS
Male	Culmen (mm)	10	78.4	1.32	19.65	2 and 35	**<0.001**	*	*	*
	Wing (mm)	10	227.0	2.29	6.56	2 and 34	**0.004**		*	
	Wing/culmen	10	2.91	0.06	7.45	2 and 34	**0.002**		*	
	Mass (g)	8	237.9	5.43	9.55	2 and 26	**0.001**	*	*	
Female	Culmen (mm)	15	97.5	1.58	42.84	2 and 41	**<0.001**	*	*	*
	Wing (mm)	14	237.3	1.69	19.06	2 and 40	**<0.001**		*	
	Wing/culmen	14	2.47	0.03	28.73	2 and 40	**<0.001**		*	*
	Mass (g)	12	307.3	7.96	7.48	2 and 25	**0.003**	*	*	

Table 2. Geographic variation in morphometrics of nonbreeding adult Bar-tailed Godwits in New Zealand. Significant results in among-region ANOVA are indicated in bold. Asterisk indicates significant result in between-region post hoc test ($P < 0.05$). Abbreviations: N = north, S = south, and C= central.

		All New Zealand			North			Central		
		n	Mean	range	*n*	Mean	SE	*n*	Mean	SE
Male	Culmen (mm)	920	83.8	69.0–98.6	593	83.5	0.24	238	84.1	0.39
	Wing (mm)	472	230.5	210–256	264	229.8	0.39	156	231.8	0.53
	Wing/culmen	461	2.73	2.31–3.32	253	2.71	0.01	156	2.77	0.01
	Mass (g)	353	277.4	194–384	197	279.5	1.55	121	276.4	2.11
Female	Culmen (mm)	862	108.9	90.0–129.0	641	108.5	0.30	168	109.8	0.58
	Wing (mm)	549	243.7	216–264	388	243.2	0.37	117	244.3	0.65
	Wing/culmen	538	2.23	1.85–2.66	377	2.23	0.01	117	2.24	0.01
	Mass (g)	343	333.2	245–400	234	333.4	1.40	81	330.3	2.41

		South			ANOVA			Tukey post hoc		
		n	mean	SE	*F*	df	*P*	N–C	N–S	C–S
Male	Culmen (mm)	89	84.8	0.66	2.28	2 and 917	0.10			
	Wing (mm)	52	230.2	0.94	4.73	2 and 469	**0.009**	*		
	Wing/culmen	52	2.74	0.03	5.60	2 and 458	**0.004**	*		
	Mass (g)	35	269.3	3.96	3.24	2 and 350	**0.040**		*	
Female	Culmen (mm)	53	111.1	1.03	4.30	2 and 859	**0.014**		*	
	Wing (mm)	44	247.0	1.08	5.90	2 and 546	**0.003**		*	
	Wing/culmen	44	2.21	0.02	0.57	2 and 535	0.57			
	Mass (g)	28	339.8	5.58	1.92	2 and 340	0.15			

longer bills compared with wing chord (wing/culmen) than males (*t*-tests, both AK and NZ: $P < 0.0001$).

Alaska.—Within AK, we found geographic variation in size for both sexes. On average, birds were largest on YKD, smallest on NS, and intermediate on SP (Table 1). Body proportions also varied geographically, and for both sexes, wing/culmen length was greatest for NS, least for YKD, and intermediate for SP. Geographic variation was strongest in culmen length: the three regions were statistically distinguishable for both sexes. SP could not consistently be distinguished from YKD and NS, but the trend of decreasing size with increasing latitude was consistent across nearly all measures.

Considering the full range of sizes present in AK, the smallest birds of each sex by culmen, wing, and mass were absent on the YKD, whereas the largest birds were absent on the NS (Fig. 3). The single exception was a conspicuously long-winged male captured on the NS; however, his other measurements were consistent with other NS males. The pattern was similar for relative wing/culmen length, as birds with extremely long wings in relation to bill did not appear on the YKD, and vice versa.

Including samples outside the three main AK regions, culmen lengths demonstrated a continuous north–south cline in both males ($r^2 = 0.390$, $F = 45.35$, $P < 0.001$, $n = 73$) and females ($r^2 = 0.474$, $F = 64.03$, $P < 0.001$, $n = 73$; Fig. 4). In addition, the slope of the line describing the cline was lower in males (slope = –0.949 ± 0.141 [SE]) than in females (slope = –1.523 ± 0.190; $t = 11.88$, df = 142, $P < 0.001$), which resulted in a progressive south-to-north reduction in sexual dimorphism of culmen length: females had 30% longer bills than males on YKD, 28% longer on SP, and 24% longer on NS. Dimorphism in wing and mass showed no latitudinal clines.

New Zealand.—In contrast to AK, we detected minimal population structure among regions in NZ, despite much larger samples (Table 2). Although southern birds of both sexes were slightly larger in mean culmen and wing, there was no consistent evidence for a north–south cline in size. Mean differences among regions were much smaller than similar comparisons within AK, with large sample sizes conferring statistical significance to differences of much lower magnitude and, presumably, less biological significance. Each NZ region contained the full range of variation in culmen and wing found in AK (Fig. 3).

Alaska vs. New Zealand.—The grand means for culmen length and wing chord in AK and NZ (Tables 1 and 2) were similar for both males (culmen: $t = 0.86$, df = 956, $P = 0.39$; wing: $t = 1.64$, df = 507, $P = 0.10$) and females (culmen: $t = 0.82$, df = 906, $P = 0.41$; wing: $t = 0.87$, df = 591, $P = 0.38$). Hence, no morphological segment of the AK population appeared to be missing from NZ. For most variables, NZ data contained extremes of distribution not found in AK, as expected given the much larger NZ samples. One exception was a northern AK female with a culmen length of 88.5 mm, smaller than the currently recognized minimum for females in NZ (90 mm). This suggests that overlap in male and female size, and consequently the number of NZ-captured godwits that are missexed, is greater than previously recognized.

Migratory departures from New Zealand.—At the Manawatu River estuary, northbound migratory departures occurred from

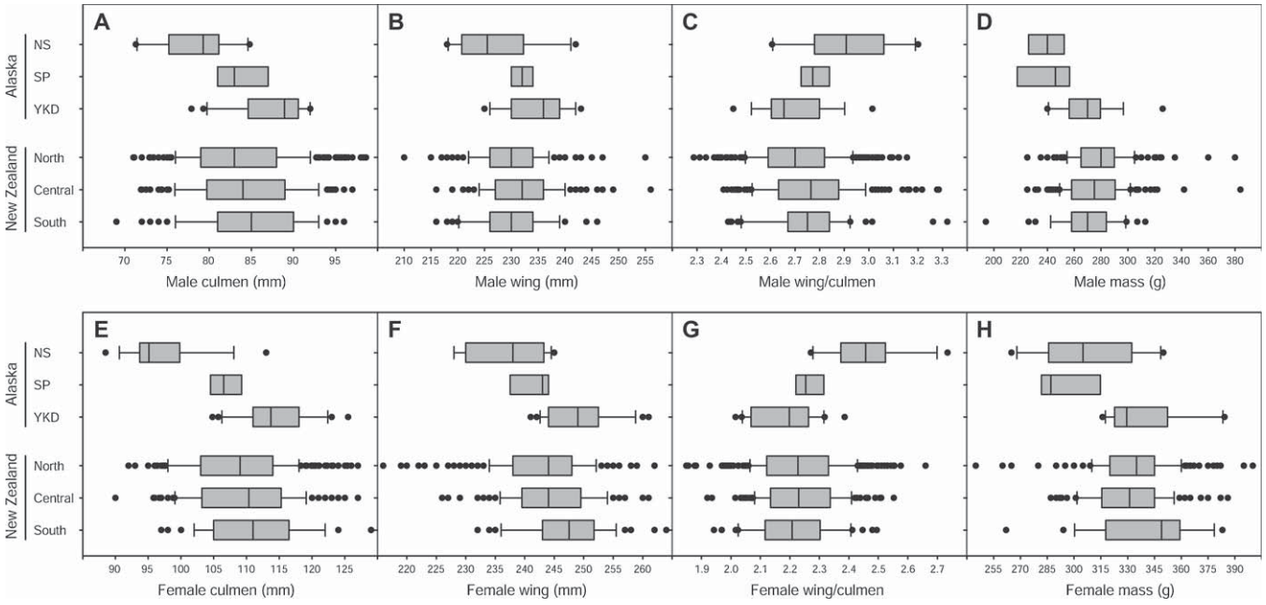

FIG. 3. Morphometrics of adult Bar-tailed Godwits by region in Alaska (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope) and New Zealand. (A) Male culmen, (B) male wing chord, (C) male wing/culmen, (D) male mass, (E) female culmen, (F) female wing chord, (G) female wing/culmen, and (H) female mass. See Tables 1 and 2 for sample sizes. Boxes indicate median and 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles.

4 March to 5 April (2008–2010). Among color-banded individuals of both sexes, larger birds departed earlier than smaller birds (mean departure date vs. culmen length; males: $r = 0.562$, $F = 15.26$, $P < 0.001$, $n = 35$; females: $r = 0.651$, $F = 28.76$, $P < 0.001$, $n = 41$; Fig. 5).

Plumage and Bill Color in Alaska

Plumage.—On average, male godwits in AK had a greater extent of breeding plumage than females in all body regions (Mann-Whitney tests, all measures: $P < 0.0001$; Table 3). For both sexes, an individual's breast plumage score was positively correlated with vent (male: $r = 0.794$, $n = 109$; female: $r = 0.810$, $n = 78$), throat (male: $r = 0.837$, $n = 108$; female: $r = 0.758$, $n = 75$), and dorsal plumage (male: $r = 0.615$, $n = 95$; female: $r = 0.587$, $n = 69$; for all tests, $P < 0.001$).

Patterns of geographic variation in plumage differed by sex. For males, extent of breeding plumage was greatest for NS and

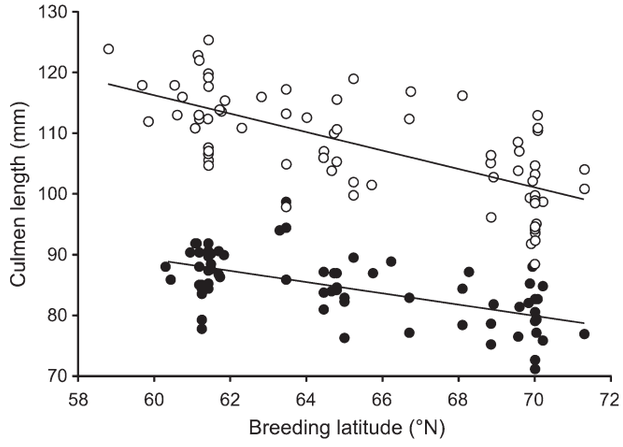

FIG. 4. Culmen length was negatively related to breeding latitude of Bar-tailed Godwits in Alaska. Includes live captures and corrected culmen lengths of museum specimens. Filled circles = males; open circles = females.

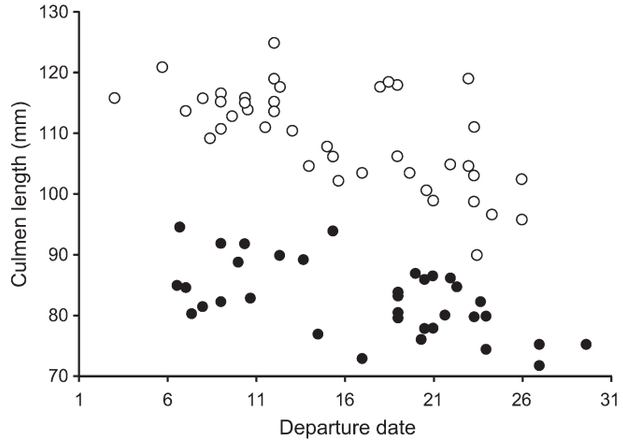

FIG. 5. Culmen length was negatively correlated with migration departure date (day 1 = 6 March) of color-banded Bar-tailed Godwits from the Manawatu River estuary, New Zealand (2008–2010). Filled circles = males; open circles = females.

Table 3. Geographic variation in plumage and bill color of breeding adult Bar-tailed Godwits in Alaska, including both live birds and museum specimens. Significant results in among-region Kruskal-Wallis test are indicated in bold. Asterisk indicates significant result in between-region post hoc test ($P < 0.05$). Abbreviations: YK = Yukon-Kuskokwim, SP = Seward Peninsula, and NS = North Slope.

		All Alaska			YK Delta			Seward Peninsula		
		n	Mean	Range	*n*	Mean	SE	*n*	Mean	SE
Male	Dorsal (%)[a]	95	92.3	65–100	25	88.2	1.78	31	93.7	0.93
	Vent (%)[a]	109	64.5	5–100	30	49.2	4.17	33	68.2	3.05
	Breast (%)[a]	111	85.7	35–100	32	74.8	2.57	33	89.9	1.76
	Throat (%)[a]	108	92.8	60–100	31	88.5	1.56	33	95.2	0.99
	Barring (0–3)[b]	99	1.00	0–3	26	1.19	0.12	32	0.69	0.12
	Bill (%)[c]	60	93.1	75–100	19	92.6	1.85	22	93.6	1.62
Female	Dorsal (%)[a]	70	78.8	20–95	14	72.5	3.51	28	86.4	0.96
	Vent (%)[a]	78	19.5	0–50	17	14.7	2.37	29	26.9	2.08
	Breast (%)[a]	80	35.4	0–80	17	24.1	2.85	30	47.5	2.96
	Throat (%)[a]	76	55.4	0–90	17	48.5	4.94	28	62.3	2.99
	Barring (0–3)[b]	74	1.74	1–3	16	1.31	0.15	28	1.68	0.14
	Bill (%)[c]	46	83.2	40–100	16	80.0	2.81	19	85.8	3.32

		North Slope			Kruskal-Wallis			Tamhane post hoc		
		n	Mean	SE	χ^2	df	*P*	YK–SP	YK–NS	SP–NS
Male	Dorsal (%)[a]	26	94.8	0.76	11.44	2	**0.003**	*	*	
	Vent (%)[a]	33	77.0	1.79	28.49	2	**<0.001**	*	*	*
	Breast (%)[a]	33	92.4	1.36	34.40	2	**<0.001**	*	*	
	Throat (%)[a]	31	95.8	1.07	17.81	2	**<0.001**	*	*	
	Barring (0–3)[b]	28	0.93	0.15	7.16	2	**0.028**	*		
	Bill (%)[c]	19	92.9	1.23	0.89	2	0.64			
Female	Dorsal (%)[a]	17	72.7	6.13	10.97	2	**0.004**	*		
	Vent (%)[a]	21	12.9	2.82	18.37	2	**<0.001**	*		*
	Breast (%)[a]	22	26.6	4.47	21.13	2	**<0.001**	*		*
	Throat (%)[a]	20	50.5	4.64	6.03	2	**0.049**			
	Barring (0–3)[b]	19	2.11	0.15	11.38	2	**0.003**		*	
	Bill (%)[c]	10	87.7	2.61	4.09	2	0.13			

[a]Values indicate proportion of breeding plumage in each body region.
[b]Values indicate amount of barring in anterior ventral region.
[c]Values indicate proportion of black color.

least for YKD (Table 3). For all plumage variables, SP males were more similar to NS than to YKD; with the exception of vent plumage, the two northern regions were statistically indistinguishable.

Among the reddest males, the great majority were found north of 64°N (Fig. 6). For example, 53% of males from SP and NS had breast scores >90%, compared with only 3% of YKD males. Conversely, only one male (1.5%) from SP–NS had a breast score <70%, whereas 22% of YKD males were in that category. A similar pattern occurred in vent scores, although far fewer males attain extensive red vent plumage; only one male (from SP) reached 100%, and 50% of YKD males scored ≤50%. Patterns in throat and dorsal plumage were less dramatic because those plumage scores showed relatively little variation; all males reached ≥60% in both throat and dorsal scores. Variation in male plumage was consistent with a north–south cline: all measures of breeding plumage demonstrated significant linear increases with latitude (vent: $r^2 = 0.258$, $n = 109$; breast: $r^2 = 0.246$, $n = 111$; throat: $r^2 = 0.116$, $n = 108$; dorsal: $r^2 = 0.128$, $n = 95$; for all tests, $P < 0.001$).

By contrast, female plumage did not conform to a north–south cline. For all breeding-plumage variables, female scores were greatest for SP, whereas YKD and NS were statistically indistinguishable (Table 3). Differences in breast plumage were most conspicuous; 43% of SP females scored >50%, compared with 9% for NS and 0% for YKD. We also found no SP females with dorsal scores <80%, whereas 35% of NS and 57% of YKD females fell in this category.

On average, females had more heavily barred underparts than males in each AK region (Table 3). For females, ventral barring increased with latitude. For males, barring was greatest for YKD and least for SP, although neither was statistically distinguishable from NS.

Bill color.—In AK, males had darker bills than females, on average (Table 3), and all birds with bills <75% black were female. Bill color did not vary significantly by geographic region for either sex. Blackness of bill was positively correlated with breast score for males ($r = 0.321$, $P = 0.013$, $n = 59$), but not for females ($r = 0.135$, $P = 0.37$, $n = 46$).

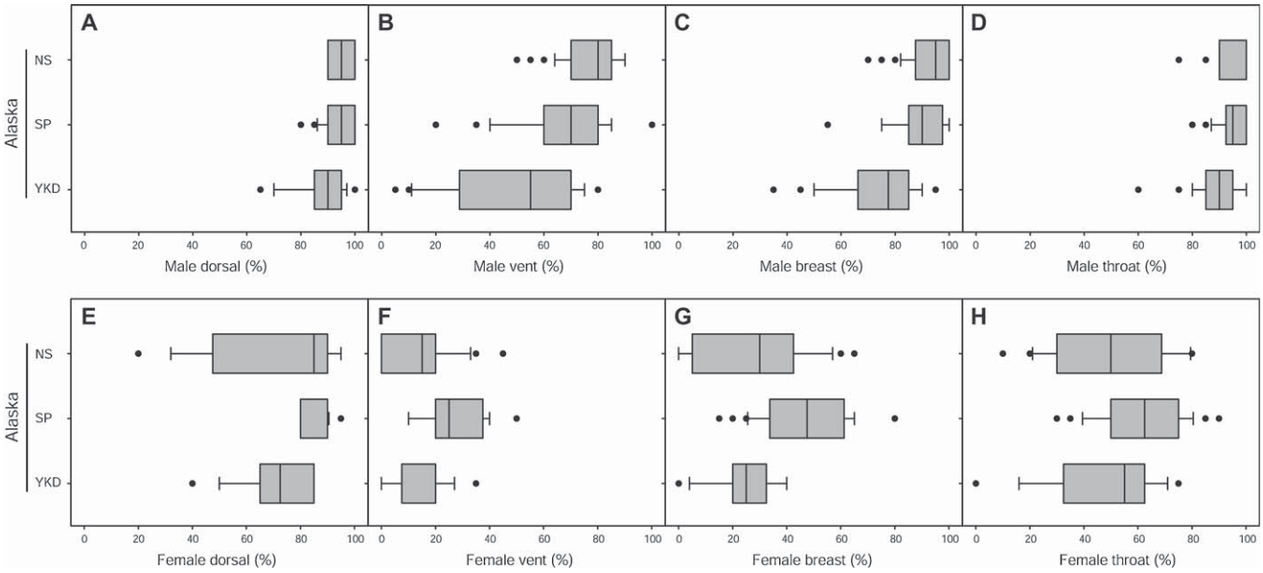

Fig. 6. Plumage of breeding adult Bar-tailed Godwits by region in Alaska (YKD = Yukon-Kuskokwim Delta, SP = Seward Peninsula, and NS = North Slope). Values indicate extent (%) of breeding plumage in each body region: (A) Male dorsal, (B) male vent, (C) male breast, (D) male throat, (E) female dorsal, (F) female vent, (G) female breast, and (H) female throat. See Table 3 for sample sizes. Boxes indicate median and 25th and 75th percentiles. Whiskers indicate 10th and 90th percentiles.

Discussion

Our study confirms and clarifies geographic variation within the breeding range of *L. l. baueri*, indications of which date back more than a century (McCaffery et al. 2011). In the only previous quantitative analysis, Rynn (1982) arbitrarily divided Alaska into two regions (at 64°N) and found regional differences in size and plumage among museum specimens of both sexes. By treating the Seward Peninsula and North Slope separately and examining linear relationships with latitude, we have demonstrated that variation in size of both sexes and in breeding plumage of males are consistent with north–south clines. However, we found no evidence that the Alaska population maintains its structure in the nonbreeding season, despite occupying a similar range of latitude in New Zealand.

Where does selection for body size occur?—No geographic variation in size was evident among New Zealand godwits. By contrast, directional selection appears to occur in the breeding season in Alaska; godwits were smaller at higher latitudes. In >70% of bird species, colder climates are associated with larger body size, but this pattern appears to be least applicable to migratory species, whose annual routines are an adaptation to avoid environmental extremes (Meiri and Dayan 2003). However, the hypothesis that migration distance limits body size is not supported by our data. The additional 1,000–1,200 km traveled to northern Alaska represents <8% of the total migration distance from New Zealand, and because northern breeders stop in southwest Alaska on both northbound and southbound migration (Conklin et al. 2010), they do not actually perform longer nonstop flights than southerly breeders.

On the breeding grounds, male godwits perform spectacular, aerobatic displays in their efforts to secure mates and territories (McCaffery and Gill 2001). These aerial displays may select for smaller males, whose greater maneuverability allows them to outperform larger males (Jehl and Murray 1986, Székely et al. 2000). In turn, if mate competition (and, thus, selection for these displays) is stronger at higher latitudes, it could foster the observed size cline in males. However, there is no evidence for geographic variation in mate competition in godwits, and this scenario fails to explain the equivalent size cline in females.

Because bill morphology is related to foraging method in probing shorebirds (Barbosa and Moreno 1999), both intra- and interspecific variation in bill length are often attributed to partitioning of prey resources (Nebel et al. 2005). Nonbreeding godwits forage primarily on mudflats, where their long bills are suited to probing for subsurface prey. By contrast, they spend the breeding season primarily on tundra, often far from mudflats, and forage primarily near or above the surface (McCaffery and Gill 2001). We therefore expect stronger selection for bill length in the nonbreeding season. However, although culmen length did not vary geographically in New Zealand, there was a cline within Alaska beyond that found in wing chord and mass; northern birds were not just shorter-billed but were proportionally shorter-billed for their size. In addition, sexual dimorphism in culmen length varied geographically, with male and female bills most similar in the north.

These findings suggest selection against long bills at high latitudes, consistent with Allen's rule (for a given body volume, surface area will be minimized in colder climates; Allen 1877). Bird bills can be a significant source of heat loss (Symonds and Tattersall 2010), and the very long bill of godwits may be a thermoregulation liability during the breeding season, particular at the highest latitudes. Alternatively, habitat differences may also contribute to geographic variation in bill length.

Why does breeding plumage vary geographically?—Broad geographic patterns within Alaska weaken the hypothesis that variation in godwit breeding plumage is primarily driven by relative individual quality and its honest signaling to rivals and mates (Piersma and Jukema 1993, Piersma et al. 2001, Drent et al. 2003). The distinct geographic patterns in male and female plumage indicate nonparallel selection acting upon the sexes, which is consistent with the assumption that male plumage plays a greater role in pair formation. However, godwit plumage has yet to be linked to basic fitness components such as reproductive success or quality of territories or mates.

One clear function of godwit plumage is nest crypsis, because both sexes incubate eggs in open ground nests (McCaffery and Gill 2001), relying on the disruptive pattern of mantle and scapular feathers to blend with the surrounding tundra. Accordingly, dorsal scores of the sexes differed by much less than ventral scores. Furthermore, dorsal plumage was the least variable plumage region within each sex, indicating similar selection across the breeding range. However, dorsal and ventral plumage covaried in both sexes, which suggests that geographic variation in dorsal plumage is not driven exclusively by adaptation to local habitats.

The patchy red and white ventral plumage of females and southern males, roughly matching tundra backgrounds (J. R. Conklin pers. obs.), may provide crypsis for non-incubating godwits. However, the striking full-red breasts of northern males are very conspicuous, drawing attention to themselves and often away from their more cryptic mates. This suggests tradeoffs between crypsis and mate acquisition that vary geographically, which could occur if competition for mates were more intense in the north, or if the brevity of the northern breeding season increased the importance of rapid mate acquisition.

Bill color may be a component of the breeding "plumage" of godwits, and thus subject to sexual selection itself, as in some passerines (e.g., Jawor et al. 2003). Alternatively, the seasonal increase in bill blackness may be an adaptation to mediate heat loss at high latitudes (Symonds and Tattersall 2010), given that black pigmentation confers greater absorption of heat. However, we found no geographic variation in bill color, despite a correlation with breast plumage in males.

Because barred feathers are a component of alternate plumage rather than the subsequent supplemental plumage, interpretation of ventral barring in Alaska is complicated, particularly for males. However, it is intriguing that ventral barring of females was consistent with a north–south cline, whereas their vent, breast, and throat scores were highest at mid-latitudes. This suggests that alternate plumage is, or was, subject to different selection than supplemental plumage. If alternate plumage represents the ancestral "breeding" plumage, subsequently replaced (in evolutionary terms) by the supplemental plumage (Jukema and Piersma 2000), the conflicting patterns may reflect selection at different points in evolutionary history. The temporal overlap of prealternate and presupplemental molts (Piersma and Jukema 1993) warrants further investigation, but geographic variation suggests that the extent of barring apparent on the nonbreeding grounds prior to most presupplemental molt (i.e., January–February) may roughly indicate a godwit's breeding region.

Population structure in the breeding season.—Geographic variation in size and plumage among Alaskan godwits is similar in magnitude to differences among recognized godwit subspecies that occupy separate migratory flyways (Rynn 1982, Engelmoer and Roselaar 1998). Within *L. l. baueri*, links between breeding latitude and migration timing (Conklin et al. 2010) indicate that morphology is linked with phenology and behavior as well. In New Zealand, godwits are extraordinarily site-faithful (P. F. Battley and J. R. Conklin unpubl. data) and have highly repeatable individual migration schedules (Battley 2006). If such behavioral rigidity extends to natal philopatry and breeding-site fidelity, segments of the Alaskan population could be reproductively isolated despite having completely overlapping nonbreeding ranges. However, latitudinal clines in size and plumage, with substantial overlap among regions, suggest no distinct geographic limits to breeding populations. Genetic analyses may elucidate the age and degree of any division within *L. l. baueri* in relation to recognized godwit subspecies.

Geographic variation within Alaska has direct relevance to the diagnosis of godwits breeding in the Anadyr region of Russia as a separate subspecies (*L. l. anadyrensis*; Engelmoer and Roselaar 1998). Tomkovich (2010) found *L. l. anadyrensis* specimens to be intermediate between *menzbieri* and *baueri* specimens in both size and plumage, and concluded that *anadyrensis* was a valid subspecies. However, his Alaska sample ($n = 5$) was entirely from YKD, where *baueri* are largest. Considering all of Alaska, the measurements of Anadyr specimens fall largely within the range of values we have presented. Geographic variation in plumage of *baueri* suggests that the separation of *anadyrensis* on the basis of plumage also warrants further investigation. Therefore, it remains plausible that Anadyr godwits represent a geographically isolated segment of *baueri*.

Is latitudinal variation within Alaska consistent with patterns in other godwit populations? Among the four recognized subspecies, extent of male breeding plumage is greater in northerly breeding races (*L. l. taymyrensis* and *menzbieri*; 63–75°N) than in southerly races (*lapponica* and *baueri*; 58–70°N), and the southernmost male *baueri* are the palest in the species (Rynn 1982). In body size, the most northerly race (*taymyrensis*) is the smallest and the most southerly (*baueri*) is the largest, but latitudinal trends are obscured by a longitudinal pattern, in which western races are smaller than eastern races (Rynn 1982, Engelmoer and Roselaar 1998). Thus, variation within Alaska may reflect more general processes, but because latitude is only an index for a suite of environmental factors (e.g., temperature, habitat type, duration of breeding season), identifying sources of selection will require detailed analysis. A comparison of *L. l. baueri* and *taymyrensis* may be instructive, for they breed across similar spans of latitude (~12°) and may contain comparable variation (but see Drent et al. 2003).

In the ecologically similar Red Knot (*Calidris canutus*), northerly populations also had redder plumage than southerly populations (Buehler and Piersma 2008). In addition, there was a negative relationship between extent of breeding plumage and migration distance, implying energetic and temporal tradeoffs between molt and migration. This latter relationship is not apparent in godwits, because the shortest-distance migrant (*L. l. lapponica*) is among the paler races, and redder males in Alaska migrate farther.

Reports of intrapopulation variation such as we have described are rare among Arctic-breeding shorebirds. Engelmoer and Roselaar (1998) identified latitudinal variation for only 1 of 14 shorebird

species, the Black-bellied Plover (*Pluvialis squatarola*). Among Alaska-breeding shorebirds, we are aware of only one other example: northern-breeding Dunlin (*Calidris alpina arcticola*) are smaller than southern breeders (*C. a. pacifica*), but these populations follow very different migration patterns (Warnock and Gill 1996).

Population structure in the nonbreeding season.—The lack of population structure in New Zealand shows that *L. l. baueri* lacks the differential migration patterns (e.g., leap-frog migration) often found to accompany structure in breeding populations (e.g., Swarth 1920, Kelly et al. 2002). Because a significant portion of the Alaska population winters in eastern Australia (McCaffery and Gill 2001), some structure may yet occur across the entire nonbreeding range. However, the morphological diversity in each New Zealand region suggests that godwits from across Alaska mix freely at nonbreeding sites.

This is consistent with geolocator data showing that individuals from the Manawatu River estuary used breeding sites spanning most of the known Alaska breeding range (59.7–70.2°N; Conklin et al. 2010). Links between migratory timing and breeding location in that study are further supported by morphological data presented here: early-departing (presumably southerly-breeding) godwits were larger (Fig. 5), in accordance with the size cline that we found within Alaska. This pattern appears to be general to New Zealand sites, because larger males also departed earlier at the Firth of Thames (although this was reported in error as the opposite relationship; Battley 2006), and the 4-week span of departures implies individuals from a wide range of breeding latitudes.

We did not examine geographic variation in plumage in New Zealand, because the correlation between plumage at departure and "ultimate" breeding plumage is unclear, as a result of the resumed presupplemental molt during a stopover of 3–5 weeks in Asia (P. F. Battley and J. R. Conklin unpubl. data). Also, plumage at departure has been studied at only two New Zealand sites (Battley 2006, present study). However, male plumage was highly variable at both sites (range of breast scores: 20–100%), which is consistent with individuals from a wide range of breeding latitudes occurring at each site.

The factors that govern nonbreeding distribution of godwits remain mysterious. Although many aspects of godwit life history, such as breeding site and migration timing, seem to be "hard-wired" and presumably heritable, nonbreeding site does not. After their first migration from Alaska, young godwits (<2 years) appear to freely roam New Zealand and eastern Australia before settling on specific sites, to which they are extraordinarily faithful as adults (P. F. Battley and J. R. Conklin unpubl. data). Identifying the social and ecological factors that govern this site "choice" may reveal patterns in an apparently random nonbreeding distribution of individuals.

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